Aerial and Aquatic Respiratory Responses to Temperature Variations in *Acmaea digitalis* and *Acmaea fenestrata*

BY

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(2 Text figures)

INTRODUCTION

Acmaea digitalis Eschscholtz, 1833 and *Acmaea fenestrata* (Reeve, 1855), two limpets commonly found on the Pacific coast, are most abundant at intertidal levels vertically separated by approximately 4 feet. Exposure periods vary widely, suggesting different respiratory responses for each species.

A number of recent workers have attempted to correlate intertidal location and distribution with aerial and aquatic respiratory activity: SANDEEN, STEPHENS & BROWN (1954), SANDISON (1966), MICALLEF & BANNISTER (1967), SANDISON (1967), BALDWIN (1968) and KINGSTON (1968). Several have worked specifically with the ecology of *Acmaea*: TEST (1945), SHOTWELL (1950), FRANK (1965), JESSEE (1968), MILLARD (1968), and MILLER (1968).

Acmaea fenestrata is generally submerged during both high tides and one low tide in the Pacific coast mixed tidal cycle, while higher level *A. digitalis* are exposed during both low tides. The purpose of this study was to compare aerial and aquatic rate of respiration of the two species, within a normal summer field temperature range, 8.5° C to 31° C (KENNY, 1968).

METHODS AND MATERIALS

Animals were collected weekly from rocks south of Yaquina Head, Oregon (44° N longitude and 124° W latitude). Collections were made during a two-hour period, one hour preceding and one hour following the lower low tide of the day during May and June 1970. *Acmaea digitalis* were taken from the +4 to the +6 foot level and *A. fenestrata* from the −1 to the +2 foot level. They were immediately transferred to containers of filtered, uv-treated sea water and maintained at 12° C in a darkened incubator for at least 22 hours. Forty-two animals (3 per vessel) were placed in 14 (15 ml GME - 130) reaction vessels in a Gilson Differential Respirometer (Model GRP 14) (GILSON, 1963). The respirometer measured oxygen consumption and allowed for carbon dioxide absorption by means of 0.2 ml 10% KOH in vessel side arms closed off by a standard taper 7/15 venting plug.

Temperature equilibrations for 4 temperatures (10°, 15°, 20°, and 25° C consecutively) were conducted for 2 hours prior to taking respirometer measurements and readings (in microliters – μl) were made at ½-hour intervals following equilibration. Respiratory rates were based on the total oxygen consumption over the 2-hour period.

The Oregon State University Control Data Corporation (Model 3300) Computer was used for all statistical analyses.

One-half of the specimens were tested for all 4 temperatures, during a 17-hour period (0700 to 2400) while the remaining specimens were tested in 2 8-hour periods. The two lowest temperatures were used on the first day and the two highest temperatures the next to facilitate detection of possible temperature stress.

Ten animals of each species were exposed to aerial and aquatic conditions. Aerial conditions were simulated by first shaking the organisms to remove excess water and then placing them on dry powder paper in dry vessels.

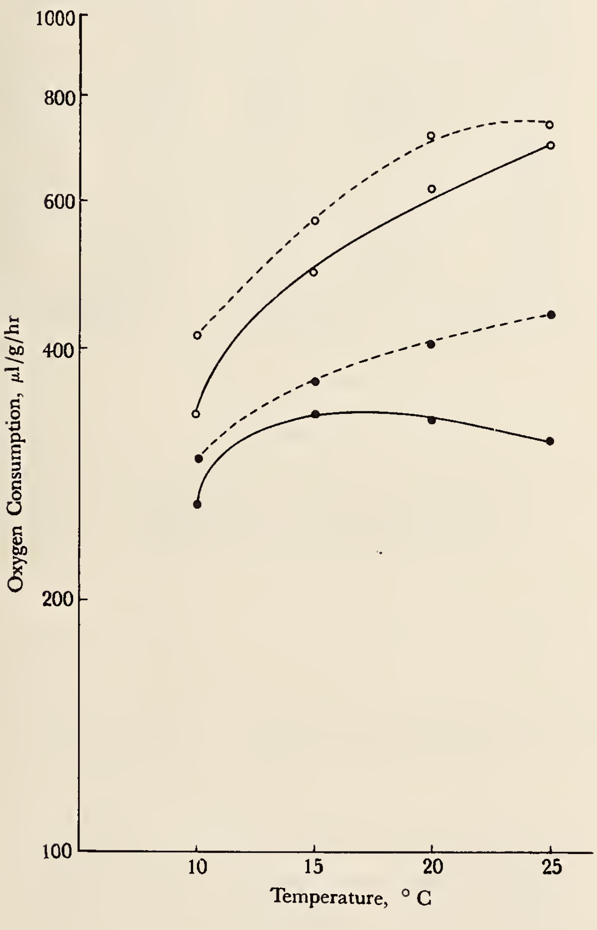

Figure 1

Oxygen consumption of *Acmaea digitalis* at temperatures between 10° C and 25° C. Average rates of oxygen uptake in air (○) and in water (●). Eight-hour trials are represented by broken lines and 17-hour trials by solid lines.

Filtered, uv-treated sea water covered the animals when aquatic oxygen consumption was determined. Experimental trials were repeated 3 times with 30 individuals of each species used at each temperature and in each of the 2 experimental conditions. The reaction vessels were agitated at 90 oscillations per minute during each trial.

After a trial, animals were removed from their shell and weighed (wet weight) on an H16 Mettler balance. They were then dried at 60° C for 24 hours and reweighed (dry weight).

RESULTS

Mean respiratory rates of the two species are shown separately in Figures 1 and 2. Four 30-minute intervals, taken consecutively during a 2-hour recording period were used to determine the mean respiratory rate. Table 1 includes the means and standard deviations.

The aerial respiration rate for *Acmaea digitalis* was consistently higher than the aquatic respiratory rate. Aerial consumption increased with rising temperatures. The rate of increase was most rapid between 10° C and 15° C and leveled off slightly from 20° C to 25° C. Aquatic consumption rates rose similarly during the 8-hour trials but at reduced levels, while during the 17-hour trials rates leveled off or decreased slightly between 15° C and 20° C.

There were no significant rate differences between aquatic and aerial respiration in *Acmaea fenestrata*. Oxygen consumption, for this species, was highest at 15° C and slowly decreased with increasing temperatures.

DISCUSSION

Data were statistically analyzed by an F-test based on values from an n-factorial analysis of variance computer program where n = 4. The 4 factors used in the analysis were: 1) the 10 replications; 2) the 2 experimental conditions – aerial and aquatic; 3) the 2 species; and 4) the 4 temperatures. Table 2 shows the F-test values used to determine statistical significance. The analysis showed significant differences in aerial and aquatic respiratory rates for *Acmaea digitalis* and no significant differences in *A. fenestrata*.

The respiratory rate of *Acmaea digitalis* during aerial conditions was significantly higher than under aquatic conditions, and respiratory peaks for each condition occurred at different temperatures (Figures 1 and 2). Aquatic rates leveled off or declined between 15° C and 20° C during the 8-hour trial. Higher temperatures may induce heat coma in this species. The occurrence of heat coma (SANDISON, 1967) may explain the difference between the aerial and aquatic respiratory responses, or the difference may simply reflect an ability of the organism

Table 2

An Analysis of Variance of the Effect of Temperature and Aerial and Aquatic Conditions on *Acmaea digitalis* and *Acmaea fenestrata*

Source of Variation	Test Value	Significance Values	Degrees of Freedom	Probability
8 hour trial				
CS	63.23	3.91	1, 144	0.05
ST	10.84	2.67	3, 144	0.05
CT	3.00	2.67	3, 144	0.05
CST	2.63	2.67	3, 144	0.05
17 hour trial				
CS	84.93	3.91	1, 144	0.05
ST	17.86	2.67	3, 144	0.05
CT	6.03	2.67	3, 144	0.05
CST	10.43	2.67	3, 144	0.05

C – Condition S – Species T – Temperature

(← adjacent column)

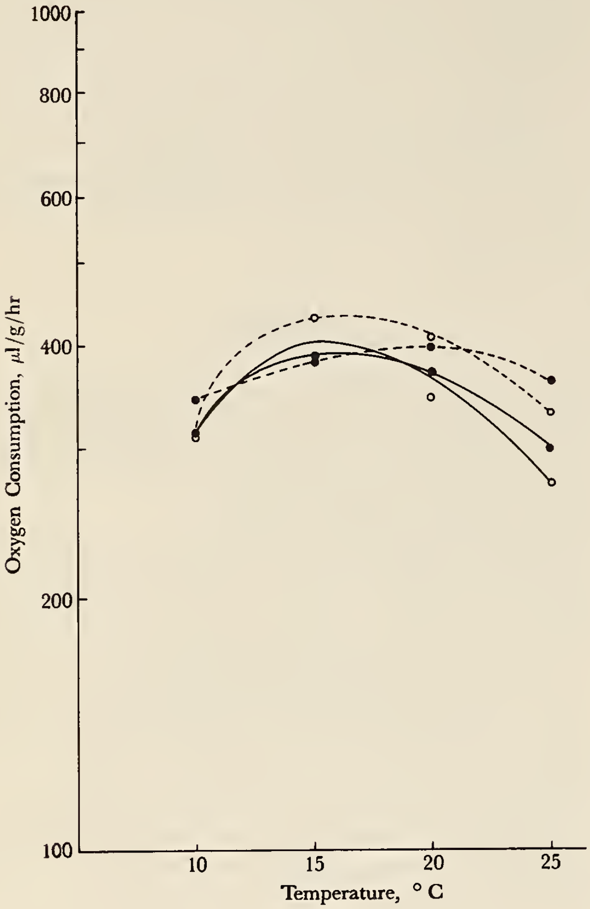

Figure 2

Oxygen consumption of *Acmaea fenestrata* at temperatures between 10° C and 25° C. Average rates of oxygen uptake in air (○) and in water (●). Eight-hour trials are represented by broken lines and 17-hour trials by solid lines.

Table 1

Mean Respiratory Rates for *Acmaea digitalis* and *Acmaea fenestrata* based on the µl of Oxygen consumed per gram (dry weight) per hour (µl/g/hr). The Means and Standard Deviations are included for each Temperature.

8 hour trial	Condition	Species	10° C	15° C	20° C	25° C
	aerial	*Acmaea digitalis*	413.45 ± 49.98	561.35 ± 64.36	718.96 ± 112.09	730.86 ± 96.82
	aerial	*Acmaea fenestrata*	307.84 ± 85.38	430.66 ± 90.49	404.41 ± 92.81	331.44 ± 103.35
	aquatic	*Acmaea digitalis*	293.08 ± 79.23	361.85 ± 113.14	404.29 ± 121.86	437.24 ± 102.42
	aquatic	*Acmaea fenestrata*	341.88 ± 65.92	378.39 ± 77.09	396.14 ± 108.60	361.36 ± 86.05
17 hour trial						
	aerial	*Acmaea digitalis*	332.94 ± 30.01	494.64 ± 39.92	621.38 ± 49.92	695.56 ± 63.77
	aerial	*Acmaea fenestrata*	308.93 ± 60.06	431.76 ± 64.04	350.37 ± 106.27	273.26 ± 104.63
	aquatic	*Acmaea digitalis*	262.21 ± 80.12	333.68 ± 121.16	326.44 ± 106.66	309.20 ± 98.36
	aquatic	*Acmaea fenestrata*	313.71 ± 69.80	388.56 ± 85.48	374.83 ± 75.25	301.11 ± 42.37

to respire more actively during aerial conditions. The principal difference between trials of different time duration was shown in the aquatic response (Figure 1). This difference could be influenced by a combination of temperature effect and duration of exposure (Orr, 1955). *Acmaea digitalis* may be exposed each day to desiccation and abrupt temperature changes (Frank, 1965). This fact was the rationale for short acclimation periods.

Hardin (1968) indicated 32° C as lethal for *Acmaea digitalis*, a value greater than our findings. However, its apparent heat coma temperature was consistent with our data (Hardin, *op. cit.*).

Evans (1948) observed normal metabolic activity in *Patella* sp. up to 30° C. Sandison (1967) found littoral marine gastropods tolerant of 6.5° C to 22.5° C; however, between 22° C and 25° C, respiratory rates increased or became very irregular (Newell & Northcroft, 1967). *Monodonta turbinata* (Micallef & Bannister, 1967), *Patella aspera* and *P. vulgata* (Davies, 1966) show irregular respiratory rates between 25° C and 33° C.

In contrast, *Acmaea digitalis* and *A. scabra* have greater oxygen consumption during aquatic conditions (Baldwin, 1968). One factor that may explain the divergent results between Baldwin's report and our findings is the difference in experimental conditions. To simulate aerial conditions, Baldwin exposed his organisms to greater desiccation. Field observations indicate that the area under the limpets' shells always retains sea water against the rock substrate. Thus, it seems that Baldwin's procedure which eliminates this type of protection would surpass the normal desiccation caused by exposed rock.

Desiccation from exposure is an important factor for limpet survival in the mid-littoral zone (Stephenson & Stephenson, 1949). Because they are situated above the lower high tide line, many individuals are exposed twice as long per day as if they were below this level (Shotwell, 1950). High surf activity and a small amount of shade most accurately characterize their microhabitat. The thick shell with a high apex, narrow ventral aperture, and relatively large water storage capacity, enables *Acmaea digitalis* to withstand drying. Behavioral adaptations such as increased nighttime activity on submerged or dampened rocks, further facilitate existence in their harsh environment.

Acmaea fenestrata, in contrast to *A. digitalis*, occupies a zone subject to shorter exposure periods and lower temperatures. Its thin, smooth shell has an almost circular ventral aperture. It follows the receding tide, and wedges its knife-like shell into the sand around and under smooth rocks where it remains moist until the return of the tide. *Acmaea fenestrata* is unique among limpets in this behavioral adaptation (Test, 1945).

The data from *Acmaea fenestrata* concur with a statement by Prosser (1950) that the thermal properties of water protect and, at the same time, fix the temperature limits of aquatic animals.

SUMMARY

Mean respiratory rates of *Acmaea digitalis* were similar to those of *A. fenestrata* at 10° C and 15° C. Significant differences occurred at 20° C and 25° C. These higher temperatures appeared to exceed the tolerance of *A. fenestrata*.

Aerial and aquatic respiratory rates did not differ significantly for *Acmaea fenestrata*. Our results indicate that 15° C is the highest tolerable temperature which is within the average summer water temperature range of 8.5° C to 16° C (Kenny, 1968).

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